

# Distribution of Microcrustacea in different habitats of a shallow lake in the Fertő-Hanság National Park, Hungary

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**Abstract.** Seventy-seven microcrustacean species (37 Cladocera, 20 Ostracoda, 20 Copepoda) were recorded from the different habitats of the small, shallow Lake Fehér (Fehér-tó) between 1998 and 2001. Significant spatial and seasonal differences were recorded in the composition of microcrustacean assemblages between the different habitats. The presence of emergent and submerged macrophytes increased predation pressure in the open water and near the shore, low oxygen content and extreme water level in the reed belt would be the main factors explaining these differences.

Habitat choice, horizontal and vertical distribution of Microcrustacea species are affected by biotic (resources and predators) and abiotic factors (dissolved oxygen, temperature, light, etc.). Submerged and emergent macrophytes have a major impact on the biological structure and species composition of shallow lakes (Scheffer & Jeppesen, 1998) and dense macrophyte beds can act as a refuge for large zooplankton species against vertebrate and invertebrate predators (Timms & Mos, 1984). In the macrophyte beds the near-edge zone is more important to migrating zooplankton than the central parts (Lauridsen & Buenk, 1996) while a low edge:area ratio would favour the non-migrating macrophyta-associated littoral species (Patterson, 1993).

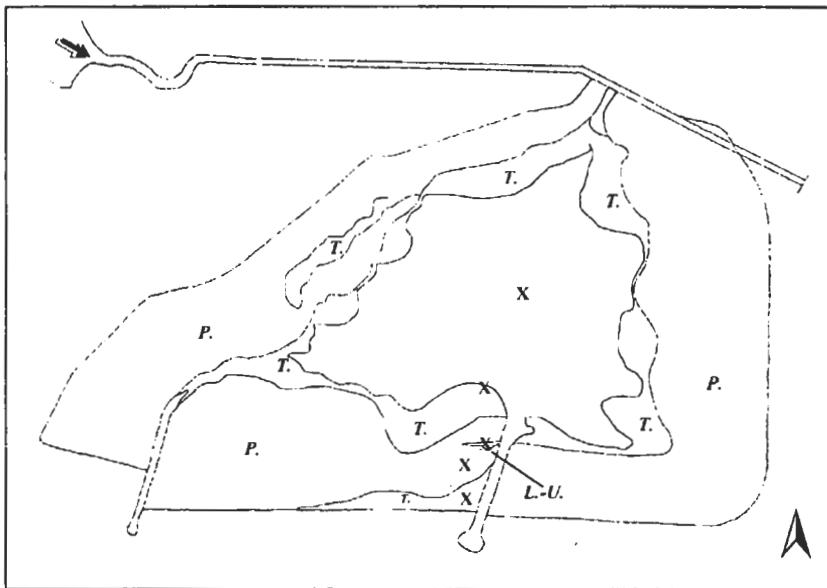
The crustacean fauna of permanently or periodically flooded reed belts has been given little attention (Löffler 1979; Forró & Metz, 1987) probably due to the rich spatial structure combined with rapidly changing environmental parameters. The Fertő-Hanság area is one of the most important wetlands in Central Europe. Limnological research has a long tradition in the Seewinkel and Lake Fertő, but only limited information is available on the hydrographically connected Hanság region. Lake Fehér is situated in the southeastern part of the Hanság Basin, it is a strictly protected area of the Fertő-Hanság Na-

tional Park. In 1998, within the frame of the Hungarian Danube Research Station, a four-year project was started to study the faunistics (Kiss, 2000, 2002), temporal and spatial distribution of several microcrustacean taxa and the composition of zooplankton assemblages in the different habitats of the lake.

## GENERAL DESCRIPTION OF THE STUDY AREA

Lake Fehér (Fehér-tó) ( $47^{\circ} 41' N$ ,  $17^{\circ} 21' E$ ) is situated in the northwestern part of Hungary, in the Fertő-Hanság National Park. It is strictly protected and not influenced by human activities. The lake is small (area:  $2.69 \text{ km}^2$ , open water:  $0.25 \text{ km}^2$ ) and very shallow (mean depth: 50 cm, maximum depth: 110 cm). The hydrology of the lake mainly depends on the interplay of precipitation and evaporation even if through a little channel there is also accidental water supply from the River Rába. The littoral zone is characterised by beds of emergent macrophytes (*Phragmites australis* and *Typha angustifolia*). From 1994 to 1997, there were no open water macrophytes in the lakes, whereas in 1999 and 2000 the open water was covered by dense vegetation of *Najas marina* (95 % PVI). In 1998 and 2001 hypertrophic conditions were recorded, dense blooms of blue-green algae developed in the lake, which was free

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**Figure 1.** Distribution of the sampling points (X) in the *Phragmites* (P), *Typha* (T) and Lemno-Utricularietum (L-U)

of open water submerged macrophytes.

Lake Fehér is a hydrocarbonated, moderately eutrophic lake. Significant temperature, pH, oxygen content and conductivity differences were measured between the open water and the reed belt (Table 1). Temperature, pH and oxygen content usually decreased while conductivity increased inshore. The open water was well-oxygenated throughout the year and becoming super-saturated in summer months as a result of photosynthesis. When *Najas marina* was present, transparency was high, suspended solid content was low and significant daily vertical differences were developed in the water column especially in temperature, pH and dissolved oxygen content values. In the turbid state (Scheffer & Jeppesen, 1998) turgidity and suspended solid content was high and there was no vertical difference in the water column. The reed belt usually dried up in

summer and early autumn. Within the reed belt, three characteristic habitat types were found: a) Scirpo-*Phragmitetum*, b) *Typhetum angustifoliae* (at the edge of the *Phragmites* zone) and between the patches of *Phragmites*, c) Lemno-Utricularietum with *Utricularia vulgaris*, *Hydrocharis morsus-ranae*, *Lemna trisulca*, *Lemna minor* and *Spirodela polyrhiza*.

Till 1983 Lake Fehér was a fish pond. Since 1983, when the area became protected, the fish stock has been considerably increased. The fish assemblage is dominated by cyprinids. The most abundant species are *Carassius auratus*, *Rutilus rutilus* and *Perca fluviatilis* (G. Guti, personal communications). Because of the low oxygen concentration and extreme water level, the reed belt is unsuitable for fish except spring when the predation pressure increase in the reed belt because of high abundance of YOY fish.

**Table 1.** Main physico-chemical parameters of the examined habitats

Parameters	Open water	<i>Najas marina</i>	Reed belt
Water depth (cm)	28-109	40-85	0-65
Temperature (°C)	0.9-31.2	15.8-22.9	1.1-23.2
pH	7.6-10.46	8.21-9.85	5.76-8.01
Oxygen content (mg/l)	2.64-20.3	2.21-18.77	0-10.79
Oxygen saturation (%)	28.6-242	14.3-226	0-100.5
Conductivity ( $\mu\text{S}/\text{cm}$ )	436-670	223-463	411-2410
Turgidity (FTU)	9-140	9-14	12-50
Suspended material (mg/l)	10-84	4-23	10-197
Soluble material (mg/l)	8-137	7-8	9-42
$\text{HCO}_3^-$ (mg/l)	0.0-442.2	0-30.6	122.2-527

## METHODS

The study was carried out from March 1998 to August 2001. Samples were collected at monthly intervals from different habitats of the lake (Fig. 1): 1. Open water (mid-lake), 2. *Najas marina* beds (mid-lake), 3. Edge of the emergent macrophyte zone, 4. Lemno-Utricularietum (narrow channel among the *Phragmites* belt), 5. *Phragmites* beds, 6. *Typha* beds. Temperature, pH, conductivity and dissolved oxygen were measured in the field by using a portable meter. Zooplankton samples were filtered through a 70  $\mu\text{m}$  mesh net then preserved in 5 % formaldehyde. In the emergent and submerged macrophyte beds microcrustaceans were collected in one litre plastic box samplers gently closed over plants. Mixed five litre samples were collected from the macrophyte beds and 50 litres from the open water and the near the edge of the *Typha* beds as well as qualitative sediment samples were also taken from different habitats of the lake with a 70  $\mu\text{m}$  mesh net.

Microcrustaceans were counted by using inverted microscopy and identified to species level. Very dense samples were subsampled. Nauplii were not taken into consideration.

## RESULT AND DISCUSSION

### Open water

Between 1998 and 2001, 36 Microcrustacea species (24 Cladocera, 4 Ostracoda, 8 Copepoda) were recorded in the open water of the lake (Table 2). The abundance of the species was low throughout the year, the maximum was 103 ind./l<sup>-1</sup> in 1999 after the decline of *Najas marina*. The composition of the zooplankton assemblages showed marked seasonal and annual differences. The zooplankton communities consisted of the following species: a) spring: *Cyclops vicinus* (1998-2000), *Daphnia cucullata* and *D. hyalina* (1999, 2000), *Chydorus sphaericus* (1999), *Bosmina longirostris* (2000), *Acanthocyclops vernalis* (2000), b) summer: *Moina brachiata*, *Diaphanosoma brachyurum*, *Acanthocyclops vernalis* and *Simocephalus vetulus* (1999 and 2000), c) autumn: *Acanthocyclops vernalis*, *Cyclops vicinus* (1998, 2000), *Alona intermedia*, *Pleuroxus aduncus* var. *coelatus* *Chydorus sphaericus* (1999), *Scapholeberis mucronata* and *Bosmina longirostris* (2000), d) winter: *Cyclops vicinus* (1998-2000), *Chydorus sphaericus*, *Bosmina longirostris* (2000). There was a significant

**Table 2.** Mean density (ind./50 l-1) of the species in the open water (O; n = 67), at the edge of the reed belt (E; n = 126), and in the reed belt (n = 65); L-U = Lemno-Utricularietum, P = Phragmites, T = Typha, S = found only in the sediment

	O	N	E	L-U	P	T	Species found only in the reed belt	Species characteristic for the reed belt, but also occurring at the edge of the reed belt	Species found in all habitats of the lake
<i>Acroperus harpae</i> (Baird, 1834)				5,65	4	2			
<i>Fabaeformiscandona balatonica</i> (Daday, 1888)				9,56					
<i>Pseudocandona rostrata</i> (Br. & Norm., 1889)				3,04	1,33	6,66			
<i>Cypridopsis vidua</i> (O. F. Müller, 1776)				1,3	23,3				
<i>Paracyclops affinis</i> (Sars, 1863)				10,43					
<i>Paracyclops poppei</i> (Rehberg, 1880)				5,65	0,66	1,33			
<i>Megacyclops gigas</i> (Claus, 1857)				55,65	7,33	6,33			
<i>Microcyclops varicans</i> (Sars, 1863)				0,86	6	23,3			
<i>Daphnia curvirostris</i> Eylmann, 1887			0,35	176	281,3	98,66			
<i>Simocephalus exspinosus</i> (Koch, 1841)			+	363,9	61,3	70,66			
<i>Ceriodaphnia megops</i> Sars, 1861			+	298,7	186	116,6			
<i>Ceridaphnia laticaudata</i> P. E. Müller, 1867			+	37,82	25,3	37,3			
<i>Megafenestra aurita</i> (Fischer, 1849)			0,18	11,73	4	6,66			
<i>Bunops sericea</i> (Daday, 1888)			0,031	39,56	10,66	16,66			
<i>Tretocephala ambigua</i> (Lilljeborg, 1900)			+	102,2	52,66	84,7			
<i>Oxyurella tenuicaudis</i> (Sars, 1862)			+	3,47		0,66			
<i>Polyphemus pediculus</i> (Linné, 1761)	1,66		+		55,33	7,3			
<i>Candonia weltneri</i> Hartwig, 1899			0,09	90,43	7,33				
<i>Fabaeformiscandona fabaeformis</i> (Fischer, 1854)			S	S	S	S			
<i>Fabaeformiscandona fragilis</i> (Hartwig, 1898)			0,031	+	1,33	6,66			
<i>Pseudocandona compressa</i> (Koch, 1838)	+		0,06	27,82	90	73,3			
<i>Candonopsis kingsleii</i> (Brady & Rob, 1870)			S	S	S	2			
<i>Cyprna ophthalmica</i> (Jurine, 1820)			+	9,13	40	9,33			
<i>Cyclocypris globosa</i> (Sars, 1863)			+	12,17	42	4,93			
<i>Cyclocypris laevis</i> (O. F. Müller, 1776)			+	16,95	77,33	78,7			
<i>Cyclocypris ovum</i> (Jurine, 1820)			0,31	790	1397	2249			
<i>Notodromas monacha</i> (O. F. Müller, 1776)			+	334,8	95,3	8,66			
<i>Carthocamptus staphylinus</i> (Jurine, 1820)	0,06		0,5	36,95	13,33	4,66			
<i>Carthocamptus microstaphylinus</i> (Wolf, 1905)			+		20,6	21,3			
<i>Mixodiaptomus kipfelwieseri</i> (Brehm, 1907)			+	0,86	4	26,7			
<i>Macrocylops albidus</i> (Jurine, 1820)	33,3		0,96	59,13					
<i>Cyclops strenuus</i> Fischer, 1851			+	319,1	422,6	620			
<i>Megacyclops virens</i> (Jurine, 1820)		31,6	7,65	642,6	220,7	403,3			
<i>Daphnia longispina</i> O. F. Müller, 1785	0,156		0,9	359,5	92	18			
<i>Daphnia hyalina</i> Leydig, 1860	7,25		1,03	0,4					
<i>Ceriodaphnia reticulata</i> (Jurine, 1820)	2,09	35	1,18	204,8	483,3	580			
<i>Simocephalus vetulus</i> (O. F. Müller, 1776)	80,81	9420	310,7	223,7	68	167,3			
<i>Scapholeberis mucronata</i> O. F. Müller, 1785	2,68	40	59,03	37,82	53,33	100,7			
<i>Alona intermedia</i> Sars, 1862	13,56	530	3,78			0,66			
<i>Alonella excisa</i> (Fische, 1854)	0,12	1,66	+	49,13	109,3	63,3			
<i>Pleuroxus aduncus</i> var. <i>coelatus</i> Weigold	10,12	315	13,31	26,52	4,66	16			
<i>Chydorus sphaericus</i> (O. F. Müller, 1785)	168,3	1810	45,87	484,8	212,6	146,7			
<i>Fabaeformiscandona protzi</i> (Hartwig, 1898)	S		S	3,91	S	2,66			
<i>Eucyclops serrulatus</i> (Fischer, 1851)	6,09	268,3	8,81	65,21	19,33	80,66			
<i>Ectocyclops phaleratus</i> (Koch, 1838)	0,09	3,33	0,09	17,82	15,33	12,66			
<i>Cyclops insignis</i> Claus, 1857	0,12		0,53	323	39,3	152,7			
<i>Diacyclops bicuspidatus</i> (Claus, 1857)	0,03		0,125	16,52	20,66	22			
<i>Mesocyclops leuckarti</i> (Claus, 1857)	8,78	460	43,4	88,26	111,3	115,3			

Table 2. (Continuation)

	O	N	E	L-U	P	T	
<i>Diaphanosoma brachyurum</i> (Liévin, 1848)	8,53	270,8	5,09				
<i>Daphnia cucullata</i> Sars, 1862	47,87	6,66	28,9				
<i>Simocephalus serrulatus</i> (Koch, 1841)	0,66	38,3	0,16				
<i>Moina brachiata</i> (Jurine, 1820)	4,59	20	6,46				
<i>Ceriodaphnia quadrangula</i> (O. F. M., 1785)	3,31	83,3	3,09				
<i>Iliocryptus sordidus</i> (Liévin, 1848)	S		S				
<i>Iliocryptus agilis</i> Kurz, 1878	S		S				
<i>Bosmina longirostris</i> (O. F. Müller, 1785)	58,62	6,66	4,84				
<i>Graptoleberis testudinaria</i> (Fischer, 1851)	83,09	2150	5,96				
<i>Leydigia acanthocerooides</i> (Fischer, 1854)	0,06	1,66	S				
<i>Alona guttata</i> Sars, 1862	0,37	5	0,15				
<i>Disparalona rostrata</i> (Koch, 1841)	S	3,33	0,16				
<i>Physocypria kraepelini</i> G.W. Müller, 1903	0,06	16,6	2,87				
<i>Cyclops vicinus</i> Uljanin, 1875	75,31	1,66	44,7				
<i>Acanthocyclops vernalis</i> (Fischer, 1853)	263,4	383,3	20,87				
<i>Daphnia pulex</i> Leydig, 1860			+				
<i>Ceriodaphnia dubia</i> Richard, 1894	0,37						
<i>Leydigia leydigi</i> (Schoedler, 1863)	S		S				
<i>Alona affinis</i> (Leydig, 1860)			+				
<i>Alona quadrangularis</i> (O. F. Müller, 1785)			+				
<i>Pseudochydorus globosus</i> (Baird, 1843)	+		+				
<i>Candonia candida</i> (O. F. Müller, 1776)			S	S			
<i>Candonia neglecta</i> Sars, 1887	S						
<i>Fabaeformiscandonia hyalina</i> (B. & R., 1870)			S				
<i>Cypridopsis elongata</i> (Kaufmann, 1900)				S			
<i>Cypridopsis hartwigi</i> Müller, 1900					1,33		
<i>Cryptocyclops bicolor</i> (Sars, 1863)						+	
<i>Macrocylops fuscus</i> (Jurine, 1820)			S				
<i>Microcycllops rubellus</i> (Lilljeborg, 1901)			+				

Species found in the open water, also occurring or common at the edge of the reed belt

Rare species found only at one or two occasions

mid-summer decline in June and at the beginning of July especially in the large-bodied cladocerans because of the increased predation pressure by the YOY fish (Luecke et al., 1990). Increased temperature and enhanced pH caused by the high photosynthetic activity of the blooming phytoplankton, decreased phytoplankton edibility and the high concentration of suspended sediment strongly affected cladoceran density and species richness during the vegetation period of the turbid state (1998, 2001). Cladocerans are generally more sensitive to elevated pH than cyclopoid copepods and increased suspended sediment content decreases the fecundity and survivorship of cladocerans via reduced ingestion rates of phyto-

plankton cells (Arruda et al., 1983). The summer presence of *Cyclops vicinus* and *Acanthocyclops vernalis* supported the finding that some cyclopoid copepods are tolerant to high pH (Hansen et al., 1991). High pH has a negative effect on fish spawning (Jeppesen et al., 1990) as well and this may result a temporary reduction of the predation pressure on filter-feeders.

*Iliocryptus sordidus*, *I. agilis*, *Leydigia leydigi*, *Disparalona rostrata*, *Candonia neglecta* and *Fabaeformiscandonia protzi* appeared only on the surface of the sediment. In contrast with the reedbelt, ostracods had a low density and species richness in all cases, and a significant part of the

individuals were juveniles. The density and species richness of ostracods increased inshore.

### *Najas marina*

In small, shallow lakes, most factors which affect zooplankton distribution are temporally variable and unpredictable, but the presence of macrophytes in the open lake markedly changed the zooplankton communities. Fish predation has a smaller impact on the zooplankton community in the more structured environment of macrophyta beds, particularly when the PVI exceeds 15-20 % (Schriver et al., 1995), and this generally invoked to explain the high density of zooplankton in vegetated habitats. In *Najas* beds the zooplankton community mainly consisted of cladoceran species and the ratio of the macrophyte-associated species was high (*Simocephalus vetulus*, *Graptoleberis tetudinaria*, *Alona intermedia*, *Pleuroxus aduncus* var. *coelatus*). In *Najas* beds a small population of *Simocephalus serrulatus* was detected for the first time in the lake in August, 2000. The mean density of the zooplankton was the largest in this habitat (530 ind./l<sup>-1</sup>) (Table 3) because of the big population of *Simocephalus vetulus* (501 ind./l<sup>-1</sup>). In *Najas* beds increased pH values and low oxygen content near the sediment (especially during night) decreases the predation risk especially the risk caused by visually hunting predators. The microcrustacean colonization of the *Najas* beds occurred gradually from the surrounding reed belt. *Ceriodaphnia reticulata*, *Graptoleberis testudinaria*, *Polypheus pediculus*, *Megacyclops viridis* and *Macrocylops albifidus* were present only in 2000 in the *Najas*, however, these species were previously detected from the reed belt. Ostracods did not become prevalent in the open water, except *Physocypria kraepelini*.

### Edge of the emergent macrophytes

The mean density of microcrustaceans was the lowest (12.38 ind./l<sup>-1</sup>) in this habitat (Table 3). Predation risk can be expected to be the highest near the vegetation surface and the edge of the vegetation belt. The edges of macrophyton beds may be sites of intense fish predation as they move inshore and offshore dielily

(Smiley & Tessier, 1998). In this habitat type a complex assemblage was formed from the pelagic species of the open water (*Moina brachiata*, *Diaphanosoma brachyurum*, *Cyclops vicinus*) and reed belt species (*Daphnia curvirostris*, *Simocephalus exspinosus*, *Bunops serricaudata*, *Tretocephala ambigua* etc.). Species richness was high, 64 out of the 77 detected species appeared in this habitat.

### Reed belt

The composition of microcrustacean assemblages remarkably differed from that of the open water because of the distinct habitat parameters (presence of emergent and submers macrophytes, lower water depth, temperature and pH, higher conductivity, decreased fish predation). Out of the detected 77 species, 33 were recorded only from the reed belt and occasionally from the edge of reed belt in low numbers. The following genera common in the open lake were missing from the reed belt: *Diaphanosoma*, *Moina*, *Iliocryptus*, *Bosmina*, *Physocypria*, *Acanthocyclops*. The abundance of the calanoid copepod, *Mixodiaptomus kupelwieseri*, was extremely low and was found only in the reed belt in winter and early spring. Considerable seasonal differences were recorded in the zooplankton composition of the three habitats types of. The dominant species were *Daphnia longispina*, *Simocephalus exspinosus*, *Chydorus sphaericus*, *Cyclocypris ovum* and *Megacyclops viridis* in spring, *Daphnia curvirostris*, *Ceriodaphnia* spp. (*reticulata*, *megops*, *laticeudata*), *Bunops serricaudata*, *Tretocephala ambigua*, *Notodromas monacha* and *Megacyclops viridis* in summer and autumn. In late autumn and winter the oxygen content was extremely low (1-2 mg/l), all species of Cladocera disappeared, but diverse cyclopoid copepod assemblages were formed from *Cyclops strenuus*, *C. insignis*, *Megacyclops viridis* and *Megacyclops gigas*. In winter occasional anaerobic condition tolerating some copepod species (*Megacyclops viridis*, *Macrocylops albifidus*, *Eucyclops serrulatus*, etc.) may survive even under ice cover successfully coping with seasonal anoxia and hypoxia (Tinson & Laybourn-Parry, 1985). The open-water, pelagic copepod *Cyclops vicinus* was replaced by *Cyclops strenuus* in the reed belt.

Unlike the open water, diverse and abundant Ostracoda assemblage developed in the reed belt.

Table 3. Mean density (ind./l<sup>-1</sup>) of zooplankton communities in the different habitats of the lake

	Cladocera	Ostracoda	Copepoda	Total
Open water	8.5	0.0032	7.08	15.58
<i>Najas marina</i>	501	0.66	29	530.6
Edge	9.8	0.067	2.52	12.38
Lemno-Utricularietum	47.48	26	32.8	106.3
<i>Phragmites</i>	31.4	34.3	18	83.7
<i>Typha</i>	25.4	49.7	29.3	104.4

The most frequent species were *Notodromas monacha* and *Cyclocypris ovum* and the ostracod *Cypridopsis hartwigi*, which is new to the fauna of Hungary, and was recorded only once from the *Phragmites* belt. Most ostracods appeared throughout the year, except the stenoterm *Notodromas monacha*, which was detected only from April to October. There was a diverse community of Candonidae (7 species) and most individuals (except *Candonia weltneri*) were recorded from sediment samples. *Physocypria kraepelini* was replaced by the closely related *Cypria ophthalmica* in the reed belt.

There was no significant difference between the zooplankton composition of Lemno-Utricularietum, *Phragmites australis* and *Typha angustifolia* (Table 3), but the abundance of some species considerably different. Most species occurred throughout the reed belt, but the abundance of the *Daphnia longispina*, *Simocephalus vetulus*, *S. exspinosus*, *Chydorus sphaericus*, *Candonia weltneri*, *Notodromas monacha*, *Cyclops insignis* and *Macrocylops albidus* was the highest in the Lemno-Utricularietum. The reduced water movement in the reed belts favoured the frequent neuston feeders *Notodromas monacha* and *Megafenestra aurita*.

The reed belt is unsuitable for fish except in spring because of the low oxygen content and extremely low water level. Invertebrates are important predators in the reed belt, and they strongly affect the composition of littoral micro-

crustaceans (Paterson, 1993). The most important predators were cyclopoid copepods (*Macrocylops albidus*, *Megacyclops viridis*, *Cyclops strenuus*) followed by tanypod chironomids, odonates and water mites.

## CONCLUSIONS

Significant spatial and seasonal differences were recorded in the composition of microcrustacean assemblages between the different habitats of Lake Fehér. The presence of emergent and submerged macrophytes, increased predation pressure in the open water and near the shore, low oxygen content and extremely low water level in the reed belt would be the main factors causing these differences.

The observed 77 species can be divided into the next categories according to their distribution, presence and absence and abundance (Table 3):

1. Frequent in the reed belt and occasionally found at the edge of the reed belt and in *Najas* beds (25 species), typical littoral species, diverse Ostracoda communities, neuston feeders (*Notodromas monacha*, *Megafenestra aurita*).
2. Species found only in the reed belt (8).
3. Frequent in the open water and the *Najas* beds but occur at the edge of the reed belt, too (15 species), pelagic species (*Cyclops vicinus*, *Moina brachiata*, *Bosmina longirostris*, *Daphnia cucullata*), mud-living species (*Iliocryptus agilis*, *I. sor-*

*didus*, *Leydigia acanthoceroides*), low Ostracoda abundance and species richness.

4. Species found in all habitats of the lake (15).

5. Rare species in the lake (14) and in Hungary as well (*Cryptocyclops bicolor*, *Pseudochydonus globosus*, *Microcyclops rubellus*); *Cypridopsis hartwigi* was new to Hungary.

Many Microcrustacea are active swimmers, they can cover large distances and can recognize a wide variety of visual and chemical cues. Consequently, there is a potential for active, individual habitat choice and microhabitat selection, which allow microcrustaceans to balance food search and predation risk adaptively.

**Acknowledgements.** This survey was supported by the Ministry for the Environment and the Hungarian Academy of Sciences.

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